Anthropogenic food resources foster the coexistence of distinct life history strategies: year-round sedentary and migratory brown bears

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Abstract: Plastic behavioral adaptation to human activities can result in the enhancement and establishment of distinct behavioral types within a population. Such inter-individual behavioral variations, if unaccounted for, can lead to biases in our understanding of species' feeding habits, movement pattern, and habitat selection. We tracked the movements of 16 adult brown bears in a small and isolated population in northeast Turkey to i) identify inter-individual behavioral variations associated with the use of a garbage dump and ii) to examine how these variations influenced ranging patterns, movements behavior and habitat selection. We identified two remarkably distinct behavioral types: bears that regularly visited the dump and remained sedentary year-round, and bears that never visited the dump and migrated 165.7 ± 20.1 km (round-trip mean cumulative distance ± SE) prior to hibernation to search for food. We demonstrated that during migratory trips, bears moved more rapidly and were less selective in habitat choice than during the sedentary phase; during the migration phase forest cover was the only important environmental characteristic. Our results thus reinforce the growing evidence that animals' use of the landscape largely changes according to movement phase. Our study shows that anthropogenic food resources can influence food habits, which can have cascading effects on movement patterns and hence habitat selection, ultimately resulting in the establishment of distinct behavioral types within a population. Identification and consideration of these behavioral types is thus fundamental for the correct implementation of evidence-based conservation strategies at the population level.

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Other titles: Bear migration and movements in a human-dominated landscape

ONLINE SUPPLEMENTARY MATERIAL

Appendix 1:

Fieldwork and collection of GPS movement data

Between September 2012 and June 2014, we captured and collared ten adult males and six adult females from a small and isolated population using spring activated foot snares (Aldrich snares, USA) baited with dead sheep. We captured bears within 1 km of the dump as well as in the forested landscape > 10 km from the dump. Because some bears captured away from the dump also visited the dump, while some bears captured in its vicinity did not visit it at all (see *Results* in the main text), we can claim that our sampling regime was not responsible for the observed dichotomy. The use of a GSM (global system for mobile communication) alarm system connected to the snares enabled us to be on site and tranquilize the bears within 20–30 minutes and so reduce the risk of injury. We tranquillized the bears using a mixture of 2.5 mg/kg tiletamine-zolazepam (*Zoletil*®, Vibrac) and 0.05 mg/kg medetomidine (*Domitor*®, Pfizer) injected via a dart fired from a CO_2-powered dart rifle (*JM Special*, Dan-Inject ApS, Denmark). All procedures were supervised by professional wildlife veterinarians, and all captured bears safely recovered from the anesthesia.

We programmed the collars to daily record one GPS location every hour. During the winter, when bears hibernate in caves or holes, the GPS typically failed to acquire satellites; therefore we only used location data collected pre-hibernation and post-hibernation in the analyses. We determined the beginning and the end of the hibernation based on activity data collected by bi-axial activity sensors embedded in the collars (data not shown) and by the sudden failure of the GPS to acquire satellites for several consecutive weeks.

Sex	Age (yrs)	Capture date	Tracking days[ξ]	Collected GPS locations	Nr clusters (mean nr. locations/cluster) [Φ]	Movement mode	% locations in roaming phase[Ψ]	Roaming days[Ψ]	Maximum displacement (m)	ϱ
F	12-14	9.6.13	507	7006	141 (7.3)	Residency	0	0	6'386	1.7
M	7	30.5.14	157	3666	118 (10.2)	Residency	0	0	15'026	2.3
M	8	17.6.14	141	3268	86 (10.2)	Residency	0	0	17'619	2.1
M	6	28.5.14	134	3011	133 (9.8)	Migratory	8.9	7	17'112	7.3
F	6-7	20.9.12	300	3307	140 (11.1)	Migratory	27.4	43	59'958	17.8
M	5	19.9.12	492	10091	337 (9.3)	Residency	0	0	21'918	3.0
M	10-12	11.6.13	328	2835	97 (8.7)	Residency	0	0	13'135	1.8
F	>15	4.10.12	590	4166*	55 (6.8)	Migratory	6.5	13	27'876	4.1**
M	4	26.9.12	488	8392	299 (11.4)	Migratory	19.0	72	107'728	12.6
M	10	11.6.13	325	5514	235 (12.2)	Migratory	27.1	66	67'174	11.5
M	5	30.5.14	156	3567	166 (10.8)	Nomadic	71.6	139	77'100	1.3
M	8-9	22.9.12	154	1787	69 (8.7)	Residency	0	0	19'896	2.7
F	8-10	30.5.13	518	6103	285 (11.1)	Migratory	16.6	25	69'824	26.3
M	9-10	5.6.14	125	2944	82 (7.8)	Residency	0	0	6'575	1.2
F	6	24.5.14	162	2981	144 (9.7)	Migratory	22.8	23	36'107	9.4
F	5-6	2.6.14	154	3526	153 (11.7)	Residency	0	0	6'381	3.1

Table: Individual characteristics, and description of movement paths. Gender, age, duration of data collection, and basic description of movement paths are given for each individual. Movement mode has been assigned by means of the net squared displacement (NSD) and ρ-values criteria. See main text for further details.

[ξ] Includes hibernation period. [Ψ] Includes stopovers. [*]Gappy data due to collar malfunctioning: the collar of this individual had a GPS acquisition rate ≈ 50%. [**] Value smaller than expected likely due to gappy data. [Φ] Refer to Appendix 4 for more details.

Appendix 2:

Net Squared Displacement

This analytical method relies on the net squared displacement (NSD) statistics combined with a non-linear hierarchical modeling framework (Börger & Fryxell, 2012). The NSD is the square of the Euclidean distance from the start of a path to a given point in the same path. Its variation over time is characterized by mathematical peculiarities in accordance to the movement mode that it represents. Four a-priori-defined functions are fitted to the NSD data and the model parameters estimated using likelihood-based mixed-effects models. Goodness-of-fit for individual subjects are calculated using the concordance correlation (CC) coefficient calculated at the subject level (i.e. for each animal). The CC measures the match between the observed and the values predicted by the models (Börger & Fryxell 2012).

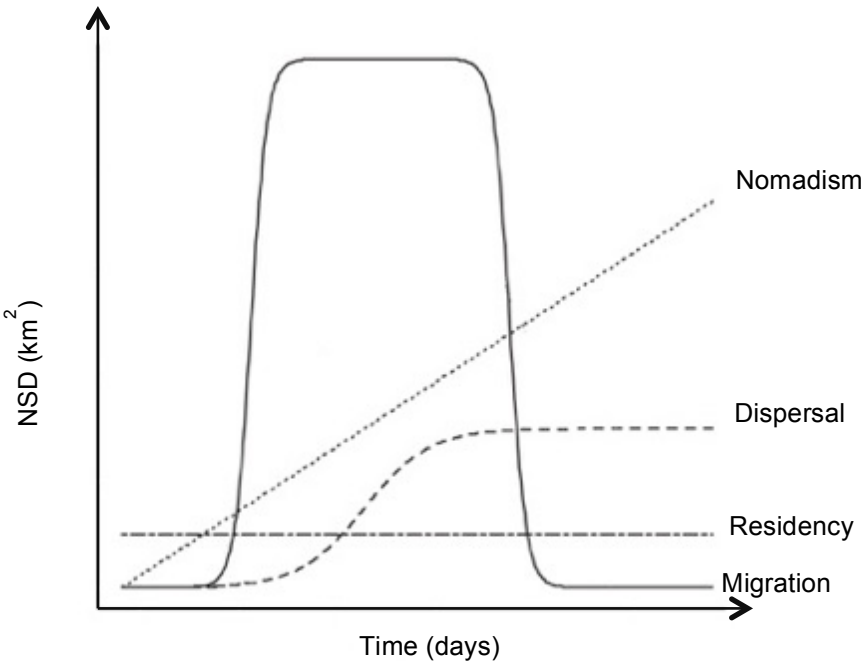


Figure: Net squared displacement (NSD) approach. Graphical representation of four a-priori-defined alternative movement modes representing i) residency all-year-round, ii) dispersal, iii) migration and iv) nomadism (modified from Bunnefeld et al. 2011).

Mathematical representation of alternative functions representing the above-depicted movement modes (Börger & Fryxell 2012) .

$$NSD_{migration} = \frac{\partial}{1 + \exp\left(\frac{\theta 1 - t}{\varphi 1}\right)} + \frac{-\partial}{1 + \exp\left(\frac{\theta 2 - t}{\varphi 2}\right)}$$

$$NSD_{dispersal} = \frac{\partial}{1 + \exp\left(\frac{\theta - t}{\varphi}\right)}$$

$$NSD_{residency} = \partial * (1 - \exp(\lambda * t))$$

$$NSD_{nomadism} = 4 * D * t$$

Parameters are as follow:

∂ = asymptotic height

θ = time at which half of the asymptotic height is reached

$\theta 1$ = for the outward trip

$\theta 2$ = for the return trip

φ = time difference between achievement of ¾ and ½ of the asymptotic height

$\varphi 1$ = for the outward trip

$\varphi 2$ = for the return trip

λ = the logarithm of the rate constant

D = diffusion constant

t = time elapsed since beginning of the path

Appendix 3:

Step selection function

We used a step selection function (SSF) framework (Fortin *et al.*, 2005; Thurfjell, Ciuti & Boyce, 2013) to infer the effects of landscape structures on bear movements during the sedentary, stopover, and roaming phases. Step selection functions incorporate animal movement properties into resource selection analyses (Fortin *et al.*, 2005). Step selection functions typically assume an exponential function of the form:

$$w(\boldsymbol{X}) = \exp(\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_n x_n)$$

where β_i are the coefficients estimated by conditional logistic regression associated with landscape variables x_i. Steps with higher SSF scores $w(\boldsymbol{X})$ are more likely to be chosen by the animals (Fortin *et al.*, 2005), and $\beta = 0$ indicates absence of selection (Forester *et al.*, 2009). We divided the entire path of each individual in independent clusters (mean = 158 clusters). A cluster had to be composed by at least five (mean = 10) consecutive locations equally spaced in time, i.e. 1 hour (cfr. Table in Appendix 2). When two observations were separated by more than 1 hour, the observations were assigned to different clusters.

To test the effect of landscape features on bears' movement and habitat selection, we created six geo-referenced raster layers that included distance to the nearest village, distance to the nearest paved road, altitude, slope, aspect, and land cover (Figure Appendix 4). Each layer fully covered the extended study area and was characterized by a cell size of 30 x 30 m. All six variables were retained for further analyses since we did not detect strong correlations ($r < 0.37$ for any pair).

We obtained a land cover map from the Turkey's Ministry of Forestry and Water Affairs at a resolution of 1:25,000 and which included two major land cover types: forest and open land. We acquired topographic information on altitude (mean: 1933 m, range: 117 – 3205 m), slope (mean: 16 degrees, range: 0 – 75 degrees) and aspect (mean: 178 degrees,

range: 0 – 360 degrees) from an ASTER Global Digital Elevation Map (http://reverb.echo.nasa.gov). We calculated the distance between each raster centroids and the closest road, the mean distance being 5'643 m (range: 0.1 – 26'499 m). Because this study was located in a rural area with very low traffic, we only considered paved national and regional roads (Turkey's Ministry of Forestry and Water Affairs). Local dirt roads are mainly used during the day by villagers on horse-drawn carriages and were assumed to have no influence on the bears' nocturnal movement behavior. Finally, we manually digitized the locations of 788 village (mean density: 1 village/20 km^2) based on an aerial Landsat image available through Google Earth. Villages were equally distributed throughout the entire study area (Online Resource 3), with mean distance between raster centroids and villages equal to 2'502 m (range: 0.5 – 11'046 m).

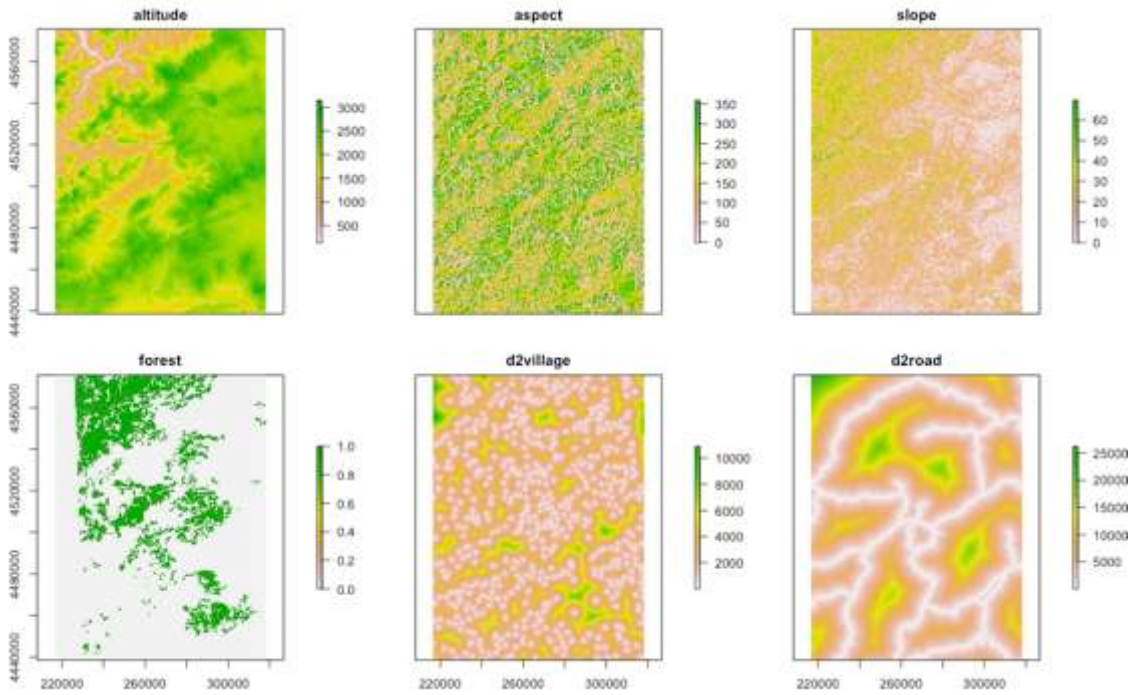


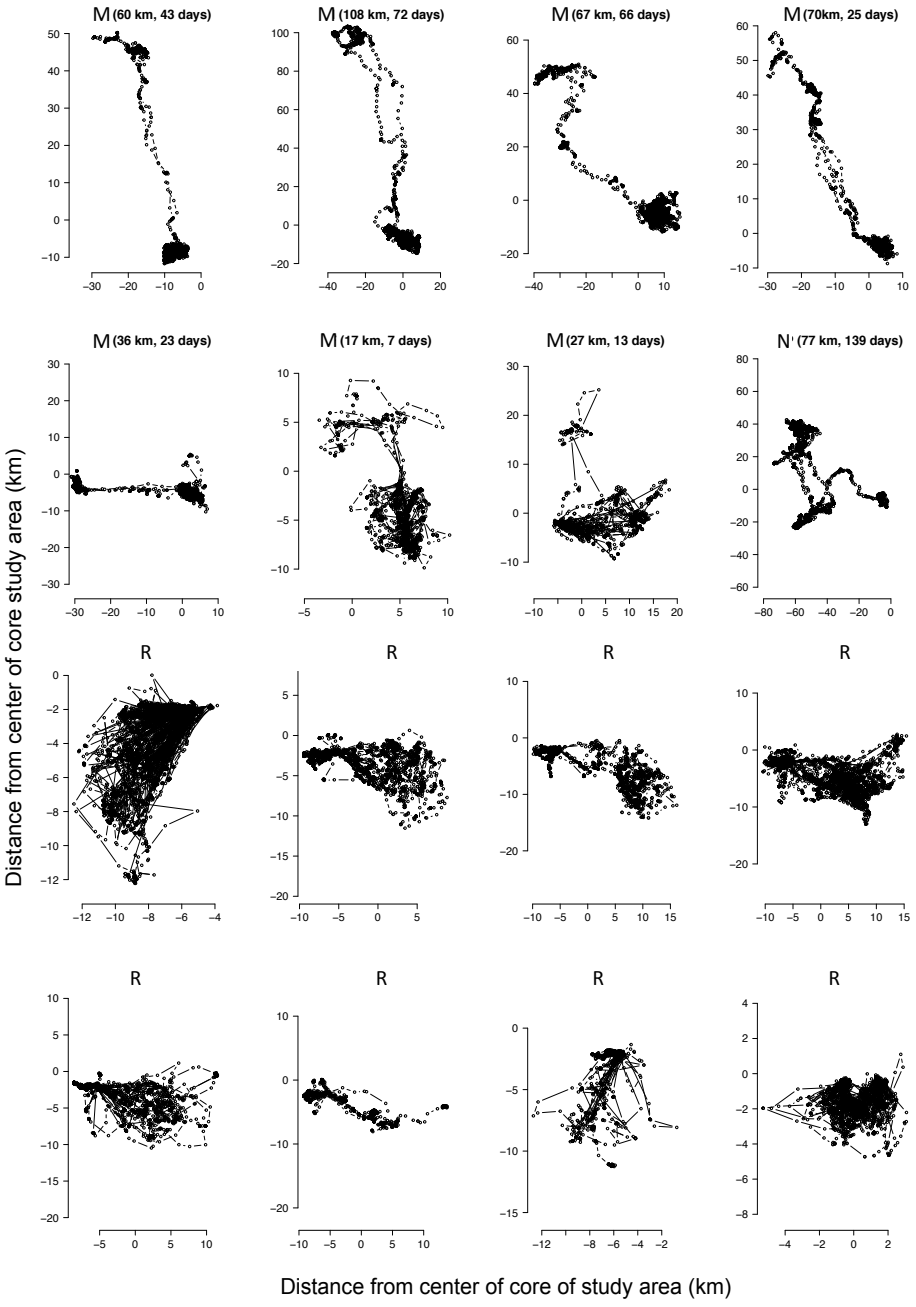
Figure: Landscape variables used to model step selection functions. Altitude, distance to nearest village (d2village) and distance to the nearest road (d2road) are given in meters; aspect and slope in degrees and forest is a factorial variable with two levels (forest or open land).

We followed the 10-fold cross-validation procedure suggested by Boyce *et al.* (2002) to examine model performance. For this, we split the data in 10 equal parts (fold), where we kept observation (i.e. used and alternative locations) from the same strata in the same fold. We then fit the model to all data except the i_{th} fold and calculated parameter estimates ($\beta_1, \ldots \beta_n$). We used the so calculated β parameters to estimate $w(\boldsymbol{X})$ values for the i_{th} fold. We repeated this procedure 10 times. We then binned the data based on the deciles of the estimated $w(X)$ values and calculated the spearman correlation coefficient (r_s) between the proportion of used locations in each bin and the mean $w(\boldsymbol{X})$ value in each bin. Using this validation method, our models provided excellent fit for the sedentary phase ($r_s = 0.95$) and only moderate for the stopover ($r_s = 0.23$) and roaming ($r_s = 0.12$) phase. For the latter two phases we caution for over interpretation of the results due to the moderate model performance. However, because this approach was developed for Resource Selection Function and not for SSF it is not necessarily clear how to account for the fact that we have stratified data when using cross-validation to validate an SSF. For this reason, these values should be taken with caution. Additionally, because during the roaming phase bears go through large non-forested landscapes (cfr. Fig. 1), depending on the random assignment of data to any of the 10 folds, some strata during the roaming phase have no used or alternative locations in forest. We did not encounter this problem with the entire dataset.

Appendix 4:

Observed movement paths.

Figure: Each dot represents a GPS location; lines connect consecutive locations. Migration (M) and nomadism (N) are shown with the relative maximum displacement and the duration of each trip. Resident movement patterns (R) are represented in the lover panel



Appendix 5

Vegetation differences between the Sarikamis forest and the stopover sites.

Because bears' migratory trips occurred right before hibernation and because direct field investigation of the vegetation at migration stopover sites revealed a prevalence of oak trees (*Quercus spp.*) forest, as opposed to the Sarikamis forest which was entirely composed of Scot's pines, we deduced that hyperphagia before the winter was the driver at the base of the observed migratory patterns.

Figure: The Sarıkamış forest is almost exclusively composed of Scots pine (*Pinus sylvestris)*. The Sarıkamış forest is heavily used for logging, grazing, harvesting and recreation. The understory vegetation is over-exploited and scarce, with consequent food scarcity for grazers (inset).

Figure: The stop over sites were characterized by a lush deciduous forest mainly constituted by oak trees as highlighted in the inset.